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SOME COMPARISONS BETWEEN VISUAL AND AUDITORY NEUROPHYSIOLOGY

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and
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Bureau of Medicine and Surgery, Navy Department
Research Work Unit MF12.524.004-9010D.04

Released by:

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SUMMARY PAGE

THE PROBLEM

To investigate and formulate new facts and theories in sensory neurophysiology.

FINDINGS

A number of instructive parallels are found between the principles and workings of the visual and the auditory systems.

APPLICATION

It is for the use of physicians, otologists, neurophysiologists who wish to keep abreast of new developments in the fields of vision and audition.

ADMINISTRATIVE INFORMATION

This investigation was conducted as a part of Bureau of Medicine and Surgery Work Unit MF12.524.004-9010D—Optimization of Auditory Performance in Submarines. The present report is No. 4 on this Work Unit. It was approved for publication on 2 September 1969, and designated as Submarine Medical Research Laboratory Report No. 592. The material was presented to the IX International Congress of Oto-Rhino-Laryngology, Mexico City, Mexico, 10-14 August, 1969.

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ABSTRACT

A number of concepts and facts from the vision domain are of interest and value to otologists. Not only the similarities but also the differences between the two sensory systems are enlightening. This paper will discuss (1) the similar ranges of sensitivity to quanta of energy and the biological mechanisms whereby the physical stimuli are transformed logarithmically, (2) coding of the physical stimulus by single cells in the optic and the auditory nerves, (3) principles of neural integration in the brainstem and midbrain nuclei (4) the point-to-point relationship between cortical activity and certain aspects of the physical stimulus, (5) the eye and ear as channels of information, and (6) cross-modality facilitation and inhibition.

SOME COMPARISONS BETWEEN VISUAL AND AUDITORY NEUROPHYSIOLOGY

Every scientist of worth who takes hearing for his domain must, of course, reckon with the fact that the body does not have one set of tissues and mechanisms for audition, another set for somatosensory perception, still another set for vision, and so on. The cells and tissues which make up our sensorium, and the biochemical, physiological, and neurological mechanisms used in one modality have their counterparts, or analogies, or at least their echoes, in every other. Of course, our sensory systems differ widely in that they are arranged some to indicate limb position, some to indicate concentration of chemical substances in the air, some to indicate the wavelength of radiant energy, etc. An overwhelming array of all sorts of information about our environment is thus picked up every moment of our lives, awake or asleep. But, the economies of Nature are such that all this is accomplished with a minimum duplication of services: the raw materials are common to all sensory systems—for example, cellular construction, graded membrane depolarization, biochemical breakdowns and equilibria, all-or-none nervous propagation, synaptic connections, types of inhibitions and suppression, sensitivity to the biological meaning of a stimulus (habituation, accentuation), and so on. Thus, it behooves workers of audition, when contemplating some unsolved problem, to consider whether a fellow-scientist in another but related field may have met that same problem and explored it in another modality.

A number of papers have pointed out the many similarities between the workings of the eye and the ear: they both deal with oscillatory phenomena, both are tuned to only a relatively small spectral range of radiant and acoustic energy, both are sensitive at their best frequency to energies as miniscule as 10^{-10} ergs per second, both have a dynamic range of about 140 decibels, both have about equivalent discrimination indices (Weber fraction) for stimulus wavelength and stimulus intensity, and so on. Thus, both the eye and the ear are responsive to wide ranges of the two main types of oscillatory energy which impinge upon us, with quite fine discriminations possible throughout these ranges. It would, therefore, in fact be surprising if the tissues and mechanisms which support these sensitivities and discriminations should not have a number of similarities which might be instructive for both vision and audition researchers to contemplate.

This paper will briefly consider some of the neurophysiological concepts which have appeared recently in studies of the two senses, pointing out what similarities and, equally informative, what dissimilarities may be found.

However, before making some general comparisons between the two nervous systems, we must first note that the older view is extremely incomplete, that is, the view that the sense organs simply transduce ambient energy to nervous energy, which is then transmitted along the primary neurone through one or more simple relay stations straight to the cortex, where it is integrated and displayed as sensory experience. On the contrary, some speak of the "little brain" within the retina, where a great deal of integration is accomplished; while the second-order neurone in audition originates in an area which is organized into at least nine separate nuclei, each with its own type of cell and destination of axon. Thus, far from looking to the cerebral cortex as the almost sole arbiter of consciousness, on the time-honored principle of the progressive encephalization of function, workers in vision and audition are looking more and more into the degree of control exercised by lower and lower centers, on what might be called the progressive de-encephalization of scientific regard. We now know that the switchboard analogy of a sensory pathway by no means exemplifies the intense and complete interplay of excitation, facilitation, lateral inhibition, suppression, adaptation, rate of spontaneous firing, spontaneous rotation of firing, "off-effects," and other neural phe-

nomena, all of which may well contribute to the probability of firing of a higher-order neuron.

Second, we must note that it is at this date possible to go far beyond static properties, into dynamic properties of the eye and ear. Static properties are those of fiber connections and their synaptic relations, determining the orderly layout of the peripheral organ onto the nuclei up to and including the cortex. The classic researches are well known on the tonotopographic layout of the auditory system, beginning with the three unrollings of the cochlea onto the cochlear nuclei, and of the point-to-point projection of the retina onto the visual cortex. The more exact definition of these pathways is still somewhat unclear, particularly the origin of primary as well as association fibers to Visual Areas II and III, and to areas other than the primary auditory projection center, but the overall pattern is clear.

On the other hand, dynamic properties go far beyond static properties in their power to explain the facts of behavior. They are concerned with (a) how environmental information is picked up and transduced by the receptor, (b) how this information is coded by the primary or first-order neurone discharge pattern, (c) how successively higher-order neurones and synaptic centers transform the first-order neurone patterns, and (d) how the higher-order centers identify the position of the stimulus in space and time, and discriminate among stimulus qualities and patterns.

Thirdly, it must not be thought that the auditory and visual nervous systems have much in common except for the fact that they use the same raw materials and the same dynamic principles. The visual system is primarily designed to display the geometry of space: it is extremely sensitive thus to the location of points, lines, edges, and more complicated patterns. Furthermore, it is a relatively slow biochemical system, responding to the order of minutes delay to brightness changes, and with a critical flicker fusion as low as 5 c/s in dim light. On the other hand, the auditory system is relatively insensitive to the geometry of space, adjusts almost instantaneously to sudden large changes in stimulus intensity, and is exquisitely sensitive to temporal patterns, with a critical fusion frequency estimated at interruptions up to 2000 per second (white noise, 0.5 on-fraction)[1]. There are then profound differences between the modalities in at least two aspects of the stimulus, namely, geometry and timing, which render them so different that it is not instructive for workers in one modality to consider how the other sense handles either geometry or time. We may, however, profitably examine other parallels. For this audience it will perhaps be more agreeable to mention some of the recent advances in visual neurophysiology, and seek to discover whether auditory neurophysiology has kept pace and if not whether we should extend our efforts in pathways blazed by our fellow-scientists in vision.

The first remarkable coincidence is that in order to handle the enormous ranges of stimulus energy, both eye and ear found it necessary to evolve two complete sense organ complexes per eye and per ear. By the turn of the century von Kries' duplicity theory of rods-cones, and the presence of inner-outer hair cells, were well known. Both the rods and the outer hair cells improve the overall sensitivity of the organism by about 40 db. Rhodopsin, the active photopigment in the rods, was discovered by Boll in 1875. Now Wald[2] and Marks, Dobelle and MacNichol[3] have shown absorption spectra for individual cones indicating that there are three cone photopigments. These substances translate the absorption of light into an electrical event. What comparable reactions are there in audition? Nothing remotely analogous has so far appeared in the hair cell. It is not even sure that the initiation of the primary neuron activity is chemical in its real nature. Davis[4] has most recently concluded that the cochlear microphonic liberates a chemical which initiates an electrical event in the dendrites of the primary neurone, but on no other grounds than Grundfest's[5] general dicta (1) that the ephapse (a synapse or synapse-like junction incorporating electrical rather than chemical transmission) is an exception and not the rule, and (2) that dendritic branches are in general electrically un-

excitable. Microelectrode studies[6] show that a dc charge of as much as 0.14 V is available between the strongly negative interior of a hair cell and the strongly positive endolymph. It does not seem improbable that charges of a very appreciable fraction of a volt might in fact stimulate the dendrites directly, without the intermediary of a chemical transmitter. Recall also Whitefield's[7] argument that we do not know the real magnitude of the potential arising from a single hair cell, because of phase differences among adjacent hair cells which tend to reduce greatly the voltage at the experimenter's electrode. Of course, the voltage of the CM itself, expressed as a ripple on this large charge, is itself infinitesimal at threshold, being of the order of 7 pV[8] (.000000007 V).

With regard to the duplicity theory, then, the different absorption spectra of the rods and cones, are not matched at all by a difference in the chemistry of the outer and inner hair cells: the hair cells seem differentiated for level of sensitivity by reason of the more rigid mechanical mounting of the inner cells, and by the more nearly one-to-one innervation of the inner cells (though it is now understood that the innervation density of the inner hair cells is far higher than that of the outer, so that 3000 primary nerve fibers serve 12,000 outer hair cells, while 27,000 serve 3500 inner cells, an innervation density ratio of 1:30 in favor of the inner cells.)

Bearing upon the non-differentiation of inner and outer hair cells also is the fact that microelectrode studies of the threshold sensitivities of a group of fibres (presumably hair cell-nerve units), tuned to the same frequency region, do not show two populations of sensitivity, one 40 db more sensitive than the other, but a single population covering a 70-80 db range.

There are of course obvious anatomical differences between the inner and outer hair cells—the globular shape of the inner cells, the well-defined "W" shape of the ciliary pattern on the outer cells, etc., but these are few compared to the manifest and manifold similarities. On the other hand, the two groups of cells do show some chemical differences; for example, the outer rows are more sensitive to the damage from streptomycin and kanamycin, and from anoxia. It would certainly not be amiss to continue to look at the chemical composition of the two groups, on the chance that they may be distinguished by separate sets of biochemical equations as are the rods and cones.

We may now look at the first electrical events, again beginning with the eye. In the electroretinogram, the first or A-wave occurs with a latency of no less than 1.7 msec[9]. However, it was known that all the physicochemical steps which lead to bleaching of rhodopsin are complete well before that period of time; thus there was a period during which electrical activity could and should have been present, but was not recorded. In 1964, Brown and Murakami[10] reported a new receptor potential of the monkey retina with no detectable latency. By placing a microelectrode on the receptor cells in the retina and using 20 microsec light flashes, they discovered an electrical event, now generally called the Early Receptor Potential (ERP), probably mediating between the photochemical reactions and the subsequent electrical responses in the first-order neurone in the retina. It is biphasic, with a latency of less than 25 microsec, and arises from the action of light on the visual pigments. This is the visual electricity which is analogous to the hair cell microphonic, for which the latency between deformation of the membrane and appearance of the CM is equally brief, a few microsec at most. The amplitudes of both the ERP and the CM are linear with stimulus intensity (i.e., + 1 log unit, either of trolands or of sound pressure level, yields 20 db output voltage increase). But while the ERP has been shown by its latency to be the result of a molecular change occurring prior to the true bleaching reaction, the CM has of course not been identified with any chemical action at all.

Beginning at about 1.5 msec latency, a second, or Later Receptor Potential (LRP), has been found in the rods and cones, and its leading edge identified with the A-wave in the normal electroretinogram (Granit's PIII component). But no second phase of the CM has ever been noted signalling any chain of

successive chemical reactions. It is of course always possible that someone following Békésy, and later Tasaki, by placing microelectrodes on the hair cells may find latencies or other characteristics which are related to chemical processes, but such a two-pronged attack and correspondence seems highly unlikely in the immediate future.

The first receptor events can only mirror in a more or less imperfect way the status of the environment; for example, the light from the pupil has to filter through 9-10 layers of retina before it reaches the rods-cones, thus being reduced about 90% by reflectance from the cornea, loss in the optical media and retinal layers[11]. Again, vibrations of the eardrum produced by faint sounds must override the very considerable noise due to blood flow, tensions on the intra-aural muscles, etc. The receptors themselves can do little more than introduce a rather simple code of the environment; their messages consequently must be elaborated and organized to support integrations and discriminations. For some purposes, such as the ability of the honeybee eye to detect the polarization of light, the receptor itself is the prime though simple organizer; but for most functions, a more elaborate system, the nervous system, is required.

Now we ask, why is the retina itself so fully furnished with neural tissue and connections? It is an immensely complicated structure, performing operations which the auditory system, for example, performs in the brainstem, leaving the cochlea relatively uncluttered. Granit suggested that it is because the microcosm of the c.n.s. in the retina can move as part of the whole eye and can participate better in the interpretation of the ever-changing brightnesses, colors, and patterns out of which the visual world is synthesized.

But then the correct analogies of the nervous layers within the retina do not reside generally in the cochlea, but in the brainstem. Perhaps the outer plexiform layer, a complicated nervous structure first after the rods-cones, has for its real analogy not the spiral ganglion in the modiolus, which seems to serve no integrative function, but the cochlear nuclei, which serve profound integrative functions. Perhaps the inner plexiform layer of the retina, the last step upstream before reaching the ganglion cells of the optic nerve fibres, has its correct analogy in the superior olivary nuclei, whose functions are just now being opened up to our inspection. The optic nerve proper therefore would not have for its analogue the auditory nerve, but the brachium of the inferior colliculus, since both would pass to the geniculate bodies and without much more reorganization, if any, straight to the cortex.

Consider, for example, the outer plexiform layer, some of its cells attaching directly to the rods-cones. Here there are horizontal cells joining cones to a larger group of rods and cones, each horizontal cell making contact by way of a separate dendritic basket with each of several rods-cones, separated by as much as 0.8 mm. Inasmuch as each foveal cone is only of the order of 1-3 mu, it can be seen that lateral action is relatively widespread. Svaetichen[12] found a special intraretinal potential, the so-called S-potential, and Mitarai[13] identified four types of S-potential, and identified two of them with the inner and outer layers of horizontal cells in the outer plexiform layer. Granit feels that the horizontal cells, which are the very first nerve cells after the rods-cones, offer the beginning of a starting loop or positive feedback system for facilitation. The counterpart in audition would be cells originating and terminating in the cochlea connecting the hair cells. Such an arrangement is unknown.

Consider, for another example, the inner plexiform layer of the retina. Polyak[14] classically describes (a) bipolar cells of four types (flat, brush, "mop" and midget), though electron microscopy cannot find these classifications useful, which terminate in the layer and connect to ganglion cells, (b) ganglion cell dendrites, and (c) axon-less or amacrine cells which extend laterally and form in fact 5-7 layers in the inner plexiform layer. It is now known that efferent fibres terminate here also. By electron microscopy, Dowling and Boycott[15] showed that a number of types of synapse can be found here, some, the so-called "syads" which connect a bipolar cell

both to a ganglion cell and to an amacrine cell, some simply connect a bipolar to an amacrine, an amacrine to an amacrine, an amacrine to a bipolar. The amacrine cells are of special interest, spreading widely through the layer and providing for lateral presynaptic interaction, which is usually inhibitory[16]. It is clear that in this layer we have a multitude of opportunities for interactions of all sorts.

If the correct analogy of the outer and inner plexiform retinal layers are the cochlear nuclei and the superior olivary nucleus complex, then auditory researchers are far ahead, since these auditory structures have been explored in great detail with microelectrode techniques.

Let us now look at what these microelectrode techniques can tell us. We speak here of the all-or-none axon spike potential. Here the visual physiologists were far ahead. Granit and Therman[18] early found visual units whose activity-recovery cycles were exceeded by flash rates, and could respond only to every other flash. This of course foreshadowed Wever's volley theory in audition. Granit also found retinal units with spontaneous rotation by pausing, and again resuming activity at random intervals. By the time these methods were used in audition, Granit[19] had found "on" fibres, "on-and-off" fibres, those with spontaneous firing inhibited by "on" but discharging at "off," and other types, about as many types as fibres. He concluded that the retina contained two mutually antagonistic systems, the "on" and "off." The "off-system" could integrate over time, so that the longer it was active, the greater would be the subsequent "off-discharge." Meanwhile, Hartline was showing lateral inhibition in the neuronal network just below the ommatidea in Limulus, as a mechanism of contrast.

Much of the truly illuminating pioneer work in vision having been done in the animal, and even the invertebrate, perhaps auditory workers would do well to spend more time on the insect, amphibian, etc., perhaps even the protozoa with cilia.

The triangular response-areas of single auditory neurones of Galambos and Davis[20] and their many followers, are well-known, but one may examine trains of spikes in many more complicated and powerful ways. In audition, these are largely due to Rosenblith: (a) threshold sensitivity, used by Galambos and Davis, (b) response latency (some units broadly tuned to spike **number** may be sharply tuned to latency of **first spike**, (c) interspike interval, as expressed by (1) interspike interval histogram, (2) scaled interval histogram, (3) joint interval histogram, and (4) an expectation density function; (d) density of firing, expressed by (1) averaged post-stimulus-time histogram (PST) or (2) density of firing during and after stimuli of different durations. Density of firing indexes are especially powerful since they give us information about the overall **responsiveness** of the unit, rather than just its **threshold sensitivity**. These two may be quite different, and give different answers to the question, to what acoustic frequency is a certain unit tuned.

Armed with the advanced computers now on most campuses, and with stable metal microelectrodes now commercially available, numbers of laboratories have studied unit spike activity to good advantage. And along with the more penetrating analysis of the unit response has gone an equal elaboration of the stimulus. What is desired, of course, is the identification of some feature of the nerve response, as coded in the ways described in the previous paragraph, with some essential feature of the stimulus. Visual physiologists have gone far beyond simple spots of light, for example, to lines, to spots and lines moving directionally, to various speeds of movement, to changes in illumination and at various rates, to edges, patterns, etc. Throughout the visual nervous system, practically all units can be stimulated either to fire or not to fire by some visual stimulus, though sometimes the experimenter has to search for a long time to find the appropriate, even unique, stimulus.

The visual unit will of course respond only to those stimuli falling on a certain area, and one can thus define a "receptive field" in the real visual world within which visual events can influence the firing rate of a higher-order

cell, if these visual events are suitable for the unit. The simplest receptive field is a circular area of excitation surrounded by a concentric inhibitory circle, and its converse in some cells, a central area of inhibition surrounded by excitation.[21]

The closest analogy in audition is the juxtaposition of excitatory and inhibitory frequency regions found by Galambos[22] and described more fully by Greenwood and Maruyama.[23] Although these areas are never exactly concentric, an excitation area may be pretty well surrounded by an inhibitory area. The analogy is of course not at all perfect, since the auditory area is a function also of stimulus intensity, while the visual field is not. But at least in the cochlear nucleus, Greenwood and Maruyama showed that the response to bands of noise, which overlap into inhibitory areas, may in fact reduce response to the noise as the band gets wider in frequency. Relevant also is the demonstration[24] of interaction among the primary or first-order auditory nerve fibers, for which no association fibers in the cochlea are definitely known.

In the visual system, only the cortex has cells with more complex receptor fields. The simplest receptor fields are not concentric circles but narrow rectangles of excitation surrounded by inhibitory fields, and the converse. Thus, the visual world is oriented by the unit, either horizontal, vertical, or oblique. For a cell with horizontal orientation, only a slit of light just the size of the excitatory area, and oriented horizontally in the external field of view will give maximum cell firing. If it is oriented vertically, then even if the stimulus does move it will elicit no response.

The picture is complicated two-fold by cells which have the same relations between excitation and inhibition but which respond not to a white rectangle on a black field but to a black rectangle on a white field.

About one-quarter of the visual cortex cells have much more complicated receptive fields, and cannot be stimulated at all by small spots of light. In **some**, only a slit of light, say $\frac{1}{8}°$ wide and 3° long, might stimulate, whereas if the slit is widened to $1\frac{1}{2}°$ it is entirely ineffective. In **some**, movement of the slit is decisive. In **some**, any slit is ineffective and only an edge of light (or dark) oriented properly will stimulate.

In audition, the response-area of frequency vs intensity is only an approximate analogue of the receptor field, since frequency as one ordinate is neurologically similar to movement in one direction, but acoustic intensity is not similar to movement in the other plane. Furthermore, complex visual receptive fields occur only in cortical units, whereas very complex acoustic stimuli are needed to stimulate many of the subcortical auditory units. For example, Kiang, et al[25] found that the activity of the second-order fiber is very much more complex than those of first-order: many second-order fibers may reduce firing as stimulus intensity grows, their response latencies may vary widely, they may have no response periods, and in general they exhibit interactions between excitation and inhibition.

Many writers have pointed out, by analogy with visual physiology, that these first intimations of the presence, indeed the ubiquitous prevalence of inhibition always strongly accompanying an excitatory area, must be taken more into account in discussing pitch discrimination, signal detection, and indeed all possible auditory contrast phenomena.

The complexity of receptor fields in the visual cortex are more than matched at a level as low as the auditory colliculus. Erulkar, et al,[26] point out that response to complex tones from units in the cochlear nuclei are predictable from responses to steady-state pure tones, but that at least at the inferior colliculus, if not the superior olive, where data are meager, a cell may be sensitive not only to a particular frequency but also differentially to rate, direction, and extent of frequency modulation, and/or to stimulus intensity changes and the rate of such change. In the visual cortex, as we have seen, complex patterns are analyzed, and in the auditory cortex likewise: a wide variety of auditory response areas, cells stimulated only by unusually-timbred transients, many cells seemingly not responsive to any auditory stimulus, etc. Furthermore, the tonotopographic and retinotopic layouts break down in the cortex at the cellular level: the rather

coarse High-Low frequency layout is well known, compared to the precision in the auditory brainstem; and even in vision, Hubel and Wiesel[21] found that closely adjacent cells did not have comparably arrayed receptor fields.

DeValois[27] found units in the geniculate separated into two kinds, so-called "broadband" cells (which gave a uniform type of response, either excitatory or inhibitory, as the case may be, to all wavelengths), and so-called "spectrally opponent" cells, (excitable to some wavelengths, inhibitory to others, with a great deal of variability in these patterns—some cells excitatory to long wavelengths, inhibitory to short, and the reverse, some differentiating intermediate wavelengths). He showed that the broadband cells respond in a lawful manner to light increases or decreases, as follows: a cell firing spontaneously to a certain light level will increase or decrease initially when the level of light increases or decreases. Then, it will adapt to its own earlier level (thus, rate of firing to any steady-state level of illumination always remains the same!). DeValois claims that this is an altogether separate system for brightness than the system of spectrally-opponent cells. Whereas in the broadband system, which is activated by cones containing more than one photo pigment, the responses of several different types of cone are being **added**, the opposite is true of the spectrally-opponent system, where the response of one type of cone is being **subtracted** from that of another.

The spectrally-opponent system for color vision obviously has no parallel in audition: the correct analogy of pitch is not color, as often assumed, but spatial location, since in both pitch change and in movement across the visual field, adjacent receptors are being successively stimulated. Just as in Granit's memorable words, "Movement of a point across the retina will light up a trail of on-off sparks," so will a frequency glissando etch an ascending series of electrical paths across the accessory nucleus, the inferior colliculus, and finally the cortex.

The whole matter of binocular and stereoscopic perception is, on the surface, very similar, but the correspondence is really only superficial. For example, DeValois shows conclusively that there is little or no binocular interaction at the geniculate, only in the cortex; while the two ears interact at the first possible level, at the terminal of the second-order fiber, and becomes hopelessly commingled for the neurophysiologist at all higher levels. That the higher centers, probably the cortex itself, is deeply involved over and above binocular interactions subcortically, is shown by Masterton and Diamond.[28] They found that cortical lesions pretty well destroyed the binaural time difference discrimination which is so critical for our everyday spatial orientation.

Some specific information is now available[21] on the effects of sensory deprivation. Kittens deprived of form but not of light during the first to third months of life, are behaviorally blind in the deprived eye, and cortical cells cannot be driven from that eye; but the geniculate is only slightly affected. However, when they are deprived of both form and light, then the geniculate also shows morphological changes. After 3 months of life, deprivation has less and less effect, until in the adult it has no effect. But this is not from disuse: when kittens were reared from months 1-3 of life with an artificial squint, but with no deprivation in either eye, connections were disrupted that served binocular interaction. Tested behaviorally, each eye appeared normal , but the usual 80% of binocularly-driven cells in the striate cortex dropped to 20%. Hubel and Wiesel conclude that "strabismus causes cells to shift in their ocular dominance, a cell coming more and more to favor the eye that dominated it at birth, ultimately losing all connection with the non-dominant eye. . . An uncorrected squint in the first few years of life leads to a permanent loss of the ability to achieve binocular vision and to a partial deficiency of visual acuity in one eye—usually in the strabismic eye."

The obvious parallel experiments in audition would be to fit one ear with a frequency-shifted hearing aid, tuning it, say, a semitone lower than the other ear, and determining later the pitch discrimination and general musicality of the person. Or shifting inter-

aural time with a delay circuit, and testing later for spatial orientation. But these experiments are still to come.

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13. ABSTRACT

A number of concepts and facts from the vision domain are of interest and value to otologists. Not only the similarities but also the differences between the two sensory systems are enlightening. This paper will discuss (1) the similar ranges of sensitivity to quanta of energy and the biological mechanisms whereby the physical stimuli are transformed logarithmically, (2) coding of the physical stimulus by single cells in the optic and the auditory nerves, (3) principles of neural integration in the brainstem and midbrain nuclei (4) the point-to-point relationship between cortical activity and certain aspects of the physical stimulus, (5) the eye and ear as channels of information, and (6) cross-modality facilitation and inhibition.

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